

LITERATURE

COMMENTS ON RECENT LITERATURE

Subspeciation in Song Sparrows. Similar species having more or less dissimilar ecological requirements frequently occur together, suggesting that they evolved side by side through a process of ecological divergence. Yet with rare exceptions, incipient species (subspecies) of a given species are not found together during the breeding season. Indeed, no very plausible genetic theory as to how a freely interbreeding, localized population could break up into races, and eventually species, has been advanced. In a review of this problem Mayr (1947) concluded that although all subspecies probably differ to some extent ecologically, geographical isolation is necessary for their evolution. Once reproductive isolation is achieved, similar species may acquire overlapping ranges. Competition between them then becomes a potent factor in promoting further ecological divergence.

Many birds once believed to be examples of ecological speciation, such as various Galapagos finches, are now thought to have passed through the usual initial stage of spatial isolation. Another group that suggests the control of speciation by ecological factors, possibly without geographic isolation, is the series of races of the Song Sparrow, *Passerella (Melospiza) melodia*, found near San Francisco Bay, some in salt or brackish marshes, others in the uplands. Thus Huxley (1942: 272) referred to them as "a case of ecotopic subspeciation in birds where the two forms are kept separate by their ecological preferences." A much needed, thorough study of these birds has now been accomplished by Marshall (1948). He personally collected more than 800 specimens during the course of his intensive field studies. These and many others were compared and measured and the stomach contents, along with other ecologically significant data, recorded.

Four races of Song Sparrows are involved. Three, *samuelis*, *pusillula*, and *maxillaris*, are found, respectively in large salt or brackish marshes north, south, and east of the Bay. The fourth, *gouldii*, is found in adjacent suitable habitats around the Bay and merges with other mainland races to the north and south. ". . . The dense bay marsh populations are separated from each other by open water or by ranges of hills jutting into the bay and are separated from upland populations by the width of the arid bayside plain" (Marshall, p. 208). Narrow connecting avenues of Song Sparrow habitat do exist between the ranges of these subspecies where, with one exception mentioned below, complete interbreeding and intergradation occur in the bird populations.

These groups of Song Sparrows thus do not differ from ordinary geographic subspecies as respects isolation but their ranges are unusually small for conti-

nenal subspecies. The sedentary habits of this abundant, resident species apparently provide sufficient isolation for this subspeciation. Even in Ohio, where many of the Song Sparrows migrate, the banding records of Mrs. Nice as interpreted by Miller (1947) indicate that most Song Sparrows settle within 300 yards of their birthplace.

The second unusual feature of these races of the Song Sparrow is the ecological diversity of the areas they inhabit. Miller (1942) had already suggested that the large number of subspecies found in the Song Sparrow as compared with, for example, the congeneric Lincoln's Sparrow, *P. lincolni*, is a result of the greater ecological tolerance of the former. The Song Sparrow is able to colonize diverse habitats; its sedentary habits then permit the evolution of races adapted to them. The habitats occupied by the Song Sparrow all possess certain characteristics vital to this species such as available water, plenty of light, plenty of vegetation within certain limits as to density, and area suitable for ground foraging. Wherever these conditions are met the Song Sparrow is at home. Thus where small areas of salt marsh are surrounded by upland habitat, the population is continuous and no racial variation is found. Along the marsh edges individual birds may feed daily on the seeds of both marsh and upland plants.

Although the individual Song Sparrow, if transplanted, would as a rule be "at home" in any of these habitats, nevertheless the racial characters of the salt marsh subspecies are presumably adaptive responses to local conditions. Where two races meet and intergrade neither is swamped out in its own habitat. Intergradation is most pronounced in the zone where the habitats themselves are intergrading. Natural selection apparently preserves the racial characters.

These rather isolated subspecies may be expected to have non-adaptive as well as adaptive genetic differences. Miller (1947) has pointed out that even in continuous populations of such a sedentary species local fixation of neutral genetic characters might occur by chance in accordance with the so-called "Sewall Wright effect." This would happen even more readily in small, isolated populations. Marshall, however, with one exception, finds the characters of the smaller or intermediate populations to vary in a gradual, predictable manner that suggests adaptive clines. His final conclusion is: "To my mind, the pronounced geographic variation shown in local Song Sparrows is but another example of this nicety of adjustment of the species to its local environments; nowhere do we find a suggestion of the gross differences in habitat preference or the qualitative differences in foraging, song and mating behavior, nor the overlap in distributions which differentiate Song Sparrows from Lincoln Sparrows and Fox Sparrows, the congeners of *Passerella melodia*" (p. 254).

It is, of course, unlikely that these Bay races of Song Sparrow will persist long enough and in sufficient isolation to become distinct species. Yet I believe that Marshall's attempt sharply to contrast their racial characters with species characters is contrary to what must normally occur in speciation and may be

occurring here. The latter suggestion is prompted by Marshall's analysis of the birds of a habitat, since destroyed, on San Francisquito Creek where the upland-willow and salt marsh habitats (and subspecies) met sharply without the usual slow transition. A series of Song Sparrows collected there about the turn of the century by Grinnell shows little hybridization, much less than would be expected if the 2 subspecies had interbred as freely as their proximity permitted. Grinnell (1901), who, incidentally, first realized the importance of these Song Sparrows as material for the study of evolution, concluded, I believe correctly, that at this point the 2 subspecies were behaving like incipient species. In races possessing adaptive modifications to rather different habitats and incipient (at least) preference for these habitats, sufficient time and isolation might well lead to speciation and the eventual acquisition of characters and behavior patterns as "qualitatively" distinct as those of such species as the Swamp Sparrow or the Seaside Sparrow.

GRINNELL, JOSEPH

- 1901 The Santa Cruz song sparrow, with notes on the salt marsh song sparrow. *Condor*, **3**: 92-93.

HUXLEY, JULIAN

- 1942 *Evolution, the modern synthesis*. Harper: London and New York.

MARSHALL, JOE T., JR.

- 1948 Ecologic races of song sparrows in the San Francisco Bay region. *Condor*, **50**: 193-215; 233-256.

MAYR, ERNST

- 1947 Ecological factors in speciation. *Evolution*, **1**: 263-288.

MILLER, ALDEN H.

- 1942 Habitat selection among higher vertebrates and its relation to intra-specific variation. *Amer. Nat.*, **76**: 25-35.
- 1947 Panmixia and population size with reference to birds. *Evolution*, **1**: 186-190.

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These comments are intended to review recent and somewhat unavailable papers covering several aspects of ornithology during the year. Your editor will appreciate remarks from Club members concerning this method of literature review.

EDITOR

BOOK REVIEWS

Birds Over America. By ROGER TORY PETERSON. Dodd, Mead and Company, New York, 1948: 7 x 10 in., XVI + 342 pp., 80 plates and one end-paper photograph. \$6.00.

Better than any other book I know, this one conveys the spirit of the enthusiast in the sport of bird study. Its pages are filled with the "shop talk" of the field ornithologist—query, speculation, anecdote of the kind we hear wherever members of the clan gather: Where is